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Function of egg punctures by Shiny Cowbirds in parasitized and nonparasitized Creamy-bellied Thrush nests

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ABSTRACT. Avian brood parasites usually remove or puncture host eggs. Several hypotheses have been proposed to explain the function of these behaviors. Removing or puncturing host eggs may enhance the efficiency of incubation of cowbird eggs (incubation-efficiency hypothesis) or reduce competition for food between cowbird and host chicks in parasitized nests (competition-reduction hypothesis) and, in nonparasitized nests, may force hosts to renest and provide cowbirds with new opportunities for parasitism when nests are too advanced to be parasitized (nest-predation hypothesis). Puncturing eggs may also allow cowbirds to assess the development of host eggs and use this information to decide whether to parasitize a nest (test-incubation hypothesis). From 1999 to 2002, we tested these hypotheses using a population of Creamy-bellied Thrushes (*Turdus amaurochalinus*) in Argentina that was heavily parasitized by Shiny Cowbirds (*Molothrus bonariensis*). We found that 56 of 94 Creamy-bellied Thrush nests (60%) found during nest building or egg laying were parasitized by Shiny Cowbirds, and the mean number of cowbird eggs per parasitized nest was 1.6 ± 0.1 ($N = 54$ nests). At least one thrush egg was punctured in 71% (40/56) of parasitized nests, and 42% (16/38) of nonparasitized nests. We found that cowbird hatching success did not differ among nests where zero, one, or two thrush eggs were punctured and that the proportion of egg punctures associated with parasitism decreased as incubation progressed. Thus, our results do not support the incubation-efficiency, nest-predation, or test-incubation hypotheses. However, the survival of cowbird chicks in our study was negatively associated with the number of thrush chicks. Thus, our results support the competition-reduction hypothesis, with Shiny Cowbirds reducing competition between their young and host chicks by puncturing host eggs in parasitized nests.

RESUMEN. **Función de la picadura de huevos por parte del tordo renegrido *Molothrus bonariensis* en nidos parasitados y no-parasitados de *Turdus amaurochalinus***

Las aves parásitas usualmente remueven o pican los huevos de sus hospedadores. Se han propuesto varias hipótesis para explicar la función de este comportamiento. El remover o picar los huevos del hospedador podría mejorar la eficiencia de la incubación de los huevos del parásito (hipótesis de la eficiencia de incubación) o reducir la competencia por comida entre los pichones del parásito y del hospedador (hipótesis de la reducción de la competencia). En nidos no parasitados en avanzado estado de incubación, podría forzar al dueño de éste a reanidar y de esta forma proveerle al tordo la oportunidad de parasitar nidos nuevos (hipótesis de depredación). La picadura de huevos podría también permitirle al tordo determinar el estado de desarrollo de los huevos del hospedador y utilizar esta información para decidir si parasita o no el nido (hipótesis de prueba del estado de incubación). Entre los años 1999 y 2002 pusimos a prueba estas hipótesis utilizando una población de Zorzal chalchalero, *Turdus amaurochalinus* en Mendoza, Argentina, que estaba siendo altamente parasitada por el tordo renegrido (*Molothrus bonariensis*). Encontramos que 56 de 94 nidos (60%) fueron parasitados durante los estadios de construcción y puesta y que el número promedio de huevos de tordo resultó ser de 1.6 ± 0.1 ($N = 54$). Al menos un huevo del zorzal fue picado en 71% (40 de 56) de los nidos parasitados y en 42% (16/38) de los no-parasitados. Encontramos que el éxito de eclosión de los huevos de tordo no fue distinto en nidos donde fueron picados cero, uno o dos huevos de hospedador y que la proporción de huevos picados asociados al parasitismo disminuyó a medida que avanzó la incubación. Por lo tanto nuestros resultados no apoyan las hipótesis de eficiencia en la incubación, depredación de nidos o estado de desarrollo de los huevos. Sin embargo, la supervivencia de los pichones de tordo estuvo asociada negativamente al número de pichones de zorzal en los nidos. Por lo cual, nuestros resultados apoyan la hipótesis de reducción de la competencia, en donde los tordos pican los huevos de la especie hospedadora para reducir la competencia entre sus pichones y los del hospedador.

Key words: brood parasitism, egg puncture, *Molothrus bonariensis*, *Turdus amaurochalinus*

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Avian brood parasites usually remove or destroy host eggs (Davies and Brooke 1988, Sealy 1992, Davies 2000, Peer 2006). For example, female Brown-headed Cowbirds (*Molothrus ater*) typically remove one host egg the day before, the same day, or the day after parasitism (Sealy 1992). Females in other cowbird species do not remove eggs, but puncture one or more host eggs. Such behavior has been observed in Shiny (*M. bonariensis*; Hoy and Ottow 1964, Post and Wiley 1977, Nakamura and Cruz 2000), Screaming (*M. rufoaxillaris*; Fraga 1998, De Mársico and Reboreda 2008), and Bronzed (*M. aeneus*; Carter 1986, Peer and Sealy 1999) cowbirds. Egg-puncturing behavior appears to have evolved at least twice in other brood parasitic lineages, including Great Spotted Cuckoos (*Clamator glandarius*; Soler et al. 1997) and Greater Honeyguides (*Indicator indicator*; Spottiswoode and Colebrook-Robjent 2007).

Several hypotheses have been proposed concerning the function of removal and puncturing of host eggs (Sealy 1992, Peer 2006). Egg removal could enhance the efficiency of incubation of the parasite egg (incubation-efficiency hypothesis; Sealy 1992, Peer and Bollinger 1997, 2000) or reduce competition for food between parasite and host chicks (competition-reduction hypothesis; Scott 1977, Blankespoor et al. 1982, Carter 1986, Mason 1986a, Sealy 1992). According to the incubation-efficiency hypothesis, removal of host eggs ensures that the parasite egg will be well incubated, and such removal would be more important when hosts are larger than the parasite because the smaller parasitic egg may not make good contact with a host's brood patch (Peer and Bollinger 1997, 2000). Consistent with this prediction, Peer and Bollinger (1997) found that eggs of Brown-headed Cowbirds translocated to nests of a host larger than the parasite (Common Grackle, *Quiscalus quiscula*) did not hatch when clutches contained four to six eggs, but hatched when clutches had three or fewer eggs. In contrast, studies of host species either similar in size or smaller than Brown-headed Cowbirds indicate that removal of host eggs did not increase hatching success of parasite eggs (Wood and Bollinger 1997, McMaster and Sealy 1997). Egg punctures could have the same effect as egg removal by a parasite if hosts remove punctured eggs as a result of nest sanitation (Kemal and Rothstein 1988). For the competition-reduction hypothesis, the benefit of removing or puncturing host eggs would also be greater when the host is larger than the parasite because host chicks generally outcompete the parasite chick (Fraga 1985, Scott and Lemon 1996, Lichtenstein 1998).

Cowbirds also remove or puncture eggs in nests they do not parasitize (Arcese et al. 1992, 1996, Nakamura and Cruz 2000, Massoni and Reboreda 2002, Peer 2006). Arcese et al. (1996) proposed that Brown-headed Cowbirds remove host eggs or nestlings from nests discovered when they are too advanced to parasitize to force renesting and provide cowbirds with new opportunities for parasitism (nest-predation hypothesis). Similarly, Peer and Sealy (1999) suggested that Bronzed Cowbirds puncture host eggs to force renesting. Yet another hypothesis to explain egg punctures in nests that are not subsequently parasitized is that cowbirds do so to assess the degree of embryonic development of the egg, and use this information to decide whether to parasitize a nest (test-incubation hypothesis; Livesey 1936, Massoni and Reboreda 1999).

Our objective was to determine the possible function(s) of egg puncturing by Shiny Cowbirds. These cowbirds frequently parasitize the nests of Creamy-bellied Thrushes (*Turdus amaurochalinus*), a host approximately 10% larger in body mass than the parasite. Because these thrushes do not reject the spotted eggs of Shiny Cowbirds (Astié and Reboreda 2005), we were able to discriminate between punctures in parasitized and nonparasitized nests. In addition, the absence of egg-rejection behavior eliminated the possibility that egg punctures were the result of "mafia-like" retaliatory behavior, that is, brood parasites enforcing acceptance by destroying eggs or nestlings of hosts that remove parasite eggs (Zahavi 1979, Soler et al. 1995, Hoover and Robinson 2007).

According to the incubation-efficiency hypothesis, we would expect a positive association between number of host eggs punctured and subsequently removed and cowbird hatching success, whereas the competition-reduction hypothesis predicts a positive association between the number of host eggs punctured and the survival rates of parasite chicks. For egg punctures not associated with parasitism, a prediction of the nest-predation hypothesis is that the proportion of host eggs punctured should be lower in parasitized than in nonparasitized nests.

In addition, more eggs should be punctured later in the incubation period than earlier. Finally, the test-incubation hypothesis predicts that egg puncturing should precede parasitism and that the proportion of punctures followed by parasitism should decrease as the incubation period progresses.

METHODS

Our study was conducted at Guaymallén (32°51′S, 68°42′W) in the Province of Mendoza, Argentina, during the 1999–2002 breeding seasons. In this area, Creamy-bellied Thrushes breed from mid-October through late December. This species is monomorphic and socially monogamous and builds open nests at heights of 1.5–3 m. Modal clutch size is three eggs (range = 3–4), incubation lasts 12–13 days, and chicks weigh 4.6 ± 0.1 (SE) g (N = 58, Astié 2004) at hatching. The mean mass of adults is 56.5 ± 0.7 g (range = 50–69 g, N = 37). The incubation period for Shiny Cowbird eggs in nests of this host is 11–13 days and the mean mass of cowbird chicks at hatching is 3.7 ± 0.1 g (N = 23, Astié 2004). Adult female cowbirds weigh about 46 g and adult males about 55 g (Mermoz and Reboreda 2003). We pooled data from different breeding seasons because we found no differences among years in the frequency and intensity of parasitism (Astié 2004).

We found most thrush nests by searching likely sites and by following adults giving alarm calls. Nests were visited every 1–2 days until young fledged or nests failed. Eggs were marked and numbered with waterproof ink in order of appearance. For each visit, we recorded the number of host and parasite eggs and whether eggs were punctured. When, between consecutive visits, a host egg was missing and the remaining eggs were intact, we assumed that the egg had been removed by the host after being punctured by a cowbird. We made this assumption because in 65% of the cases (N = 55 nests) where we observed a host egg punctured, the egg disappeared within 24 h. We recognized eggs punctured by Shiny Cowbirds because they had one relatively large, usually triangular, hole in the eggshell (Massoni et al. 2006, Tuero et al. 2007).

Puncturing host eggs associated with parasitism. To determine if puncturing host eggs increased cowbird hatching success, we used nests parasitized once during days 0–3 (day 0 corresponds to the laying of the first host egg) and where the number of host eggs laid was three (N = 27). In this sample, the host removed all punctured eggs. We compared the hatching success of cowbird eggs (0 or 1) in nests with 0–2 punctured host eggs.

To determine if puncturing host eggs increased the survival of cowbird chicks, we used nests where: (1) only one cowbird chick hatched, (2) cowbird hatching occurred within a day of hatching of the first host chick, (3) the nest survived at least 5 days after hatching of the cowbird chick, and (4) failure of thrush eggs to hatch was due to puncturing by cowbirds (N = 21). We assumed that cowbird chicks that survived until the fifth day would have fledged if the nest had not been predated because, in 24 of 25 nests (96%) where a cowbird chick died due to brood reduction, it occurred before the fifth day (Astié and Reboreda 2006). We used this criterion because more than 50% of the nests that reached the nestling stage were predated and, therefore, few nests fledged cowbird chicks. We compared the survival of Shiny Cowbird chicks in nests where there were 0–3 thrush chicks (surrogate inverse measure of the number of host eggs previously punctured).

Puncturing host eggs not associated with parasitism. To test the hypothesis that the function of puncturing host eggs was to cause renesting, we compared the number of punctured eggs for each puncture event (one puncture event = one Shiny Cowbird visit to a nest) that was either associated or not associated with parasitism. For this analysis, we used nests: (1) where we knew the day when the first host egg was laid (day 0) and the days when punctures and parasitism (if the nest was parasitized) occurred, (2) with three thrush eggs present when egg punctures occurred (i.e., the female had completed the clutch and no eggs had been punctured previously), and (3) that were not predated for at least 2 days after the puncture event (N = 28). We considered a puncture event to be associated with parasitism when it occurred during the period from 2 days before to 2 days after parasitism (in most cases, punctures occurred either the same day as or the day before parasitism; see Results).

We also examined the number of eggs punctured as incubation progressed. We included nests where we knew the day that incubation started and the day the puncture event occurred ($N = 49$). We divided the incubation period into five 3-day stages, starting with day 0 and ending on day 14.

To test the hypothesis that cowbirds punctured host eggs to assess the degree of development of host eggs, we compared the proportion of puncture events that were either followed or not by parasitism as laying and incubation progressed. For this analysis, we used nests where we knew the day when the first host egg was laid, the days when punctures and parasitism (if the nest was parasitized) occurred, and that remained active for at least 2 days after the puncture event ($N = 50$).

Statistical analyses. We used nonparametric statistics due to lack of normality of the data and relatively small sample sizes (Siegel and Castellan 1988). Statistical tests were performed using StatView 5.0 (SAS Institute Inc., Cary, NC 1998) with $P < 0.05$ (two-tails). Values reported are means ± SE.

RESULTS

We found that 56 of 94 Creamy-bellied Thrush nests (60%) found during nest building or egg laying were parasitized by Shiny Cowbirds, and the mean number of cowbird eggs per parasitized nest was 1.6 ± 0.1 ($N = 54$ nests). At least one thrush egg was punctured in 71% (40/56) of parasitized nests, and 42% (16/38) of nonparasitized nests. Approximately 53% of the puncture events occurred during laying (days 0–2), and 32% during early incubation (days 3–5).

Puncturing host eggs associated with parasitism. To determine if puncturing host eggs increased the efficiency of incubation of cowbird eggs, we compared hatching success for nests where different number of host eggs were punctured and subsequently removed with a log-linear analysis. Cowbird hatching success did not differ between nests where zero, one, or two thrush eggs were punctured ($P = 0.94$, Table 1). For these three groups, the timing of laying of Shiny Cowbird eggs did not differ ($H_2 = 0.7$, $P = 0.69$).

To determine if there was an association between puncturing host eggs and the survival of cowbird chicks, we used logistic regression with survival of the cowbird chick as a dependent variable and number of thrush chicks (surrogate inverse measure of the number of host eggs previously punctured) as an independent variable. The survival of cowbird chicks was negatively associated with the number of thrush chicks ($\chi^2_1 = 5.9$, $P = 0.01$, $N = 21$; Fig. 1).

We also compared the tendency of Shiny Cowbirds to puncture host versus parasite eggs. For this analysis, we used nests parasitized prior to the puncturing of eggs ($N = 30$). In these nests, Shiny Cowbirds punctured a greater proportion of host (36/72) than parasite (8/48) eggs ($\chi^2_1 = 12.4$, $P = 0.01$).

Puncturing host eggs not associated with parasitism. To test the nest-predation hypothesis, we compared the number of host eggs punctured in nests where punctures were or were not associated with parasitism. The mean number of punctured eggs associated (1.86 ± 0.34;

Table 1. Hatching success of Shiny Cowbirds in Creamy-bellied Thrush nests with one cowbird egg and where zero, one, or two host eggs, respectively, were punctured and subsequently removed.

Number of host eggs punctured	Cowbird hatching success (%)	Time of laying[a] (days ± SE)	Number of nests
0	60.0	0.9 ± 0.4	10
1	53.8	1.3 ± 0.4	13
2	66.7	1.1 ± 0.5	6

[a]Relative to day 0 (laying of first host egg).

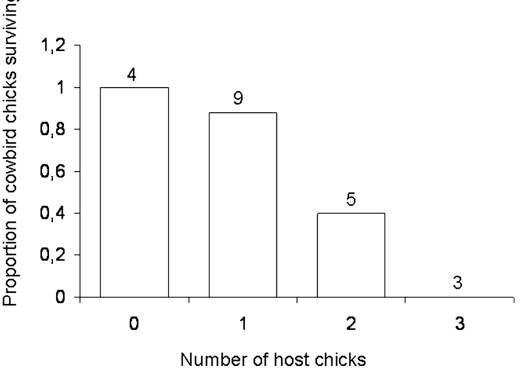

Fig. 1. Proportion of Shiny Cowbird chicks that survived until day 5 (mean ± SE) in nests with one cowbird chick and zero, one, two, or three Creamy-bellied Thrush chicks, respectively. Numbers above bars indicate the number of nests in each group.

$N = 7$) and not associated (1.38 ± 0.13; $N = 21$) with parasitism did not differ ($U' = 96$, $Z = 1.4$, $P = 0.17$). Because our sample size was small, we repeated our analysis including nests that had two thrush eggs at the time egg punctures occurred (i.e., nests where laying was not complete). This analysis also revealed no difference ($U' = 281.5$, $Z = 0.7$, $P = 0.49$) in the mean number of punctured eggs associated (1.53 ± 0.17, $N = 17$) and not associated (1.37 ± 0.10, $N = 30$) with parasitism. In addition, we found no difference in the number of host eggs punctured during the five 3-day stages of the incubation period ($H = 7.1$, $P = 0.13$, $N = 49$).

We also evaluated the predictions of the "test of incubation hypothesis." We found that 20 puncture events were associated and 30 were not associated with parasitism. All punctures of eggs in parasitized nests occurred either on the same day (17/20, or 85%) or the day before (3/20, or 15%) a nest was parasitized. To test another prediction of this hypothesis, we used logistic regression with parasitism as a dependent variable and day of the nesting cycle when the host egg was punctured as an independent variable. The frequency of puncture events associated with parasitism ($N = 50$) decreased as incubation progressed ($\chi^2_1 = 6.4$, $P = 0.01$; Fig. 2).

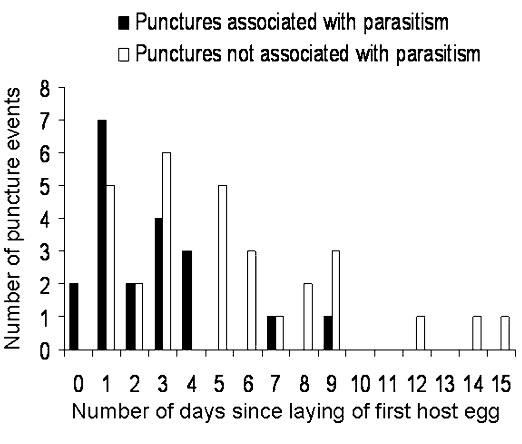

Fig. 2. Number of puncture events (in one Shiny Cowbird visit to a nest and when host eggs were punctured during the same day or the day after parasitism) associated (full bars) and not associated (open bars) with parasitism. Day 0 corresponds to the day the first host egg was laid.

DISCUSSION

Our results indicate that puncturing Creamy-bellied Thrush eggs did not enhance the efficiency of incubation of Shiny Cowbird eggs, but did increase survival of cowbird chicks. We found no difference in the hatching success of Shiny Cowbird eggs in nests with 1–3 host eggs (i.e., nests with 0–2 host eggs punctured). Our results agree with those of Wood and Bollinger (1997) and McMaster and Sealy (1997), but these studies involved hosts either similar in size or smaller than the brood parasite. In these species, the removal or puncture of host eggs would be less critical for the parasite because their larger eggs would still contact the host's brood patch (Peer and Bollinger 1997, 2000). Peer and Bollinger (1997) found that the hatching success of Brown-headed Cowbird eggs in nests of a large host (Common Grackle) was lower in large clutches. However, differences in the size of Common Grackle and Brown-headed Cowbird eggs are greater than those between the eggs of Creamy-bellied Thrushes and Shiny Cowbirds (Common Grackle eggs are 120% larger than Brown-headed Cowbird eggs, whereas Creamy-bellied Thrush eggs are 40% larger than Shiny Cowbird eggs; Peer and Bollinger 1997, Astié and Reboreda 2005). Therefore, one explanation for the differences between our results and those of Peer and Bollinger (1997) is that the removal or puncture of host eggs could enhance the efficiency of incubation of cowbird eggs only in hosts much larger than the parasite.

We found that the main benefit of puncturing Creamy-bellied Thrush eggs was the enhanced survival of Shiny Cowbird chicks. Previous investigators have found that survival of Shiny Cowbird chicks is low in hosts larger than the parasite (Fraga 1985, Lichtenstein 1998; but see Mermoz and Reboreda 2003) and that, by puncturing host eggs, cowbirds could increase the survival of their chicks in nests of larger hosts (Fiorini et al. 2009). Shiny Cowbird chicks had a higher probability of survival in nests where there were either no or one Creamy-bellied Thrush chicks (i.e., two or three host eggs had been punctured). However, the number of thrush eggs punctured per Shiny Cowbird parasitic event is approximately 0.5 (Astié and Reboreda 2006). One explanation for this apparent contradiction is that puncturing thrush eggs increases the survival of cowbird chicks, but also increases the likelihood of nest failure because nests with eggs punctured were predated more frequently (Astié and Reboreda 2006) and, therefore, there may be a trade-off between enhancing the success of the egg and the survival of the nest.

We also found that when there were both host and parasite eggs in nests at the time egg punctures occurred (i.e., punctures in nests that had been parasitized previously), Shiny Cowbirds punctured a greater proportion of host than parasite eggs. Possible explanations for such behavior include: (1) Shiny Cowbirds discriminate between host and parasite eggs and preferentially puncture the eggs of the stronger competitor (Llambías et al. 2006), i.e., the Creamy-bellied Thrush, (2) female Shiny Cowbirds may commonly lay multiple eggs in the same nest (e.g., McLaren et al. 2003) and they recognize and avoid puncturing their own eggs, and (3) female Shiny Cowbirds puncture eggs at random and, because cowbird eggs are smaller, rounder, and have a thicker eggshell (Spaw and Rohwer 1987, Rahn et al. 1988, Mermoz and Ornelas 2004), they are less likely to be punctured.

Concerning egg punctures in nonparasitized nests, our results were consistent with the predictions of the test-incubation hypothesis because egg punctures preceded or were simultaneous with parasitism, and the proportion of puncture events followed by parasitism decreased as incubation progressed. However, approximately 40% of the puncture events that occurred during egg laying and early incubation (days 0–4) were not followed by parasitism, suggesting that there may be other factors that influence egg puncturing behavior in nonparasitized nests.

Brown-headed and Shiny cowbird chicks may benefit from the presence of host nestlings because the presence of more nestlings may increase adult provisioning rates, so young parasites grow more rapidly (Kilner 2003, Kilner et al. 2004, Fiorini et al. 2009). Brown-headed Cowbirds often parasitize hosts that are smaller than the parasite (Lowther 1993, Strausberger and Ashley 1997). In such cases, the benefit of egg removal in terms of increasing the survival of the parasite chick would be less critical because host chicks are not strong competitors for the parasite. In contrast, Shiny Cowbirds frequently parasitize hosts that are larger than the parasite (Mason 1986a, 1986b, Wiley 1988). In these cases, host chicks often outcompete the parasite chicks for food (Fraga 1985, Lichtenstein 1998, Fiorini et al. 2009). Other life history traits of hosts, such as a large clutch size and a long incubation period, can also influence the survival of cowbird chicks in nests of large hosts. For hosts with these characteristics, parasite females usually have more time to sychronize egg laying with that of the host and, as a result, parasite chicks can hatch 2 or 3 days before the host chicks, increasing their chances of survival (Mermoz and Reboreda 2003).

The reproductive success of Shiny Cowbirds parasitizing Creamy-bellied Thrush nests is low because the incubation periods of both species are similar, cowbird chicks are smaller than thrush chicks when they hatch, and Creamy-bellied Thrushes often suffer brood reduction (Astié and Reboreda 2009). Therefore, with this host, puncturing eggs may be critical for enhancing the survival of Shiny Cowbird chicks. More generally, puncturing eggs may be an important strategy for some parasites because such behavior could increase the survival of parasite chicks when hosts are larger than the parasite (Fiorini et al. 2009) and when host traits decrease the likelihood that parasite chicks will survive (Astié and Reboreda 2009).

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